VOLUME XXVII NUMBER 6

# BOTANICAL GAZETTE

JUNE 1899

## PODOPHYLLUM PELTATUM.

### A MORPHOLOGICAL STUDY.

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(WITH FIGURES 1–10)

*Podophyllum peltatum* L., the *Anapodophyllon canadense* of Tournefort,[1] is a common inhabitant of the rich woods in the eastern parts of North America, ranging from Ontario to Florida and eastern Texas. On account of its social occurrence and very conspicuous foliage it is one of the most characteristic sylvan types of American vegetation. Outside of North America it has but three congeners: *Podophyllum Emodi* (Himalayas), *P. versipelle* (China), and *P. pleianthum* (China), which are the only species recognized by botanists, although Rafinesque described two others: *P. montanum* from the Alleghany mountains, and *P. callicarpum* from Louisiana and Texas. Judging from the description the last of these appears to be a good species, but has evidently not been collected by any one but Rafinesque.

While the genus is commonly regarded as a member of the Berberideæ it exhibits but very few characters common to the principal representatives of this order. It appears altogether as

[1] The derivation of Podophyllum, erroneously given in the *Synoptical Flora of North America*, p. 72, as "probably in reference to the very large footstock (!) of the radical leaves," depends evidently upon the abbreviation of its former name "Anapodophyllon" by Linnaeus. It is as stated by Tournefort "quasi planta cujus folia ad pedem Anatis accedunt," and the leaf-blade does show some resemblance to the web-foot of a duck. The reason why Linnaeus changed the name may be found in his *Critica botanica*, where similar generic names are abbreviated by "detruncatio capitis:" Oreoselinum = Selinum; Melocactus = Cactus; Anapodophyllum = *Podophyllum;* Hydroceratophyllum = Ceratophyllum.

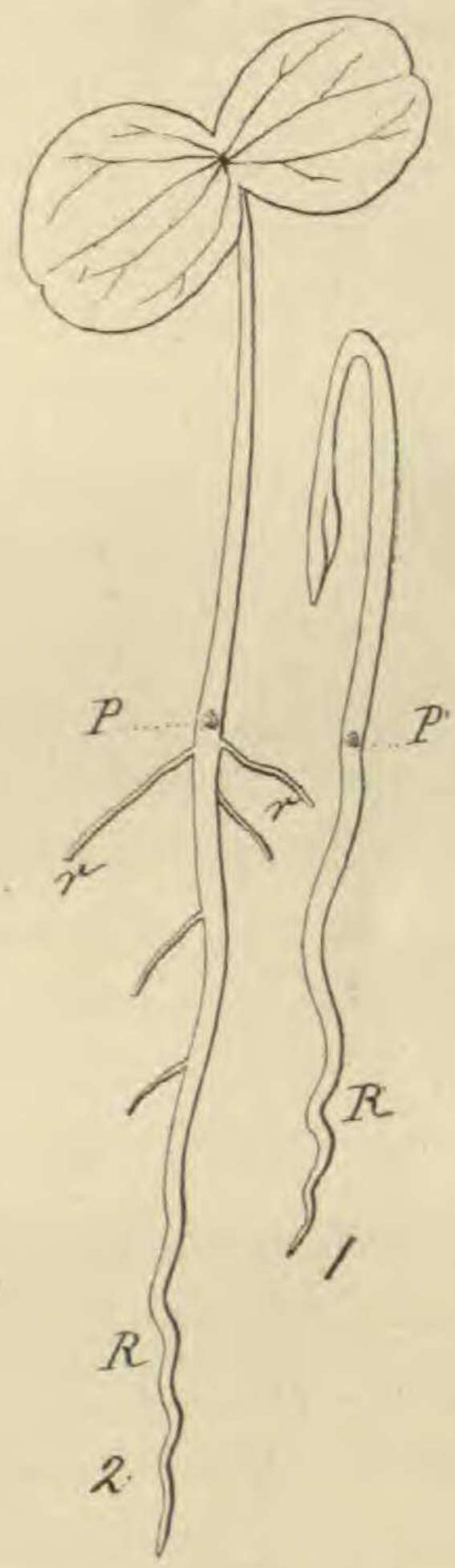
if the Berberideæ do not constitute a very natural order, even if we exclude Akebia and the other Lardizabaleæ. With Berberis as the type, it seems unnatural that this order should also comprise genera of such peculiar habit and structure as Podophyllum, Jeffersonia, Achlys and Diphylleia. At least Podophyllum shows several affinities with Actæa, and was placed next to it by Jussieu and St. Hilaire[2] under Ranunculaceæ. Another view was held by A. P. De Candolle, who placed the genus together with Jeffersonia and Achlys in his seventh order, Podophylleæ, referring Diphylleia to his Berberideæ, together with Berberis, Nandina, Leontice, Caulophyllum, etc. Baillon included Diphylleia under the order Podophylleæ. Lindley considered Podophyllum and Jeffersonia as representing a suborder, Podophylleæ, of the Ranunculaceæ. But the majority of the other authors seemed to have no difficulty in considering these genera as representing only one order, the Berberideæ. Even Asa Gray, who had better opportunities to examine the North American genera than anyone else, classified them all in the one order.

It is true, however, that the floral structure of some of these genera shows certain analogies, as demonstrated by Bentham and Hooker, and more especially by Eichler in his comprehensive work, *Blüthendiagramme;* but there are, nevertheless, other points to be taken into consideration, as for instance, the structure of the vegetative organs, if not the very habit itself, which is exceedingly variable in these genera. In regard to *Podophyllum peltatum* very little has been published concerning its vegetative propagation, and nothing of its germination. These two phases of plant life seem to be very closely connected in the perennial herbs, inasmuch as the study of their seedlings has shown us that these, in many instances, give us a figure of the full-grown plant on a small scale. In this respect *Podophyllum peltatum* illustrates several points of interest, and we shall attempt in the present article to show the various stages of development which we have observed in this plant from seedling to flowering specimen, besides a few abnormal cases.

The seeds of *Podophyllum peltatum* germinate in the early

[2] For references consult the bibliography appended to this article.

spring, the cotyledons becoming visible by the end of April. At this stage (*fig. 1*) the seedling shows a well-developed primary root, *R*, and two cotyledons, the blades of which are folded around each other and borne upon long petioles, which are united to their full length so as to form a cylindrical, hollow tube. The plumule, *P*, is very minute and located at the bottom of the cotyledonar tube. *Fig. 2* shows another seedling at a more advanced stage, in which the cotyledons have become unfolded so as to show their final shape, broadly elliptical with the apex slightly emarginate. The primary root, *R*, has begun to branch with a pair of lateral roots, *r*, developed close beneath the plumule, *P*, and a few others farther down. The cotyledonar sheath, formerly bent in order to penetrate the ground, has stretched itself and is still enclosing the plumule. This last stage is maintained by the seedling during the first year, and when the cotyledons finally decay during the fall, the plumule shows no further development; hence the cotyledons are the only assimilating leaves of the plant during its first year of growth. A similar manner of germinating, with the plumule inactive during the first year, is also characteristic of *Hydrastis Canadensis* (Ranunculaceæ), but the petioles of the cotyledons are free, very long, and slender.




FIGS. 1 and 2. Seedlings of *Podophyllum peltatum;* natural size. Explanation in text.

In *Podophyllum Emodi*, the germination of which has been studied by A. Dickson, the plumule may develop during the first season, and the first leaf is green, with a long petiole and peltate blade. No scale-like leaves are figured or mentioned. It is strange that Sir John Lubbock, who gives a similar account and illustration of *P. Emodi*, does not seem to have known of Professor Dickson's paper upon this subject, and

we are almost inclined to believe that the early development of the plumule in *P. Emodi* was simply due to cultivation in a hot-house, and that both authors have overlooked the scale-like leaves. The manner of germinating which we have described as characteristic of *P. peltatum*, with its plumule concealed, makes it very difficult for the observer to discover such seedlings in their native haunts. The color of the cotyledons is, as we remember it, of the same light green as the foliage of this plant, and it is not uncommon to meet with these seedlings growing in dense clumps. It was this last circumstance that led the writer on the right track, when, some years ago, he was looking for seedlings of this plant, which grows abundantly in the vicinity of Washington. Bearing the fact in mind that the fruit of Podophyllum falls without bursting, and with the seeds closely imbedded in the gelatinous pulp, it was natural to suspect the light green seedlings which were growing in small clumps to belong to this genus, even though the plumule showed no signs of further development.

This type of germination, with the plumule inclosed in the tubular sheath formed by the union of the petioles, is not, however, characteristic of Podophyllum alone. In looking through the vast literature that deals with the germination of dicotyledonous plants, we find several instances recorded, which remind us of Podophyllum. Among the Berberideæ themselves, *Leontice Altaica* and *L. vesicaria* show a similar development of a cotyledonar tube, as described by Bernhardi; a larger number of cases have been observed in the Ranunculaceæ, viz., species of Anemone, Ranunculus, Delphinium, Aconitum, and Eranthis; in the Umbelliferae, viz., species of Ferulago, Prangos, Smyrnium, Bunium, and *Chærophyllum bulbosum;* besides these may be noticed *Megarrhiza Californica*, *Limnanthes Douglasii*, *Rheum Moorcroftianum*, *Polygonum Bistorta*, *P. viviparum*, and *Dodecatheon Meadia.* All these cases are somewhat similar to what we have described above for Podophyllum, but with the exceptions of Eranthis, *Aconitum Anthora*, and *Ranunculus parnassifolius*, the plumule develops during the first year, breaking through the base of the tube.

There is one point, however, by which *Podophyllum peltatum* seems to differ from the plants enumerated above, and this

consists in the development of the first three leaves of the plumule as scales, the "Niederblätter" of the Germans. In all the other instances where a cotyledonar tube is developed, the first leaf of the plumule seems to be above ground, green, and of approximately the same outline as the later developed leaves. A very few cases are known from other genera, in which the first leaves are scale-like; for instance, *Hepatica triloba* and several species of Asarum, but the plumule is above ground in these, and the cotyledons are free. A very remarkable case is the germination of *Adoxa moschatellina*, which has been described by Alexander Braun. In this the cotyledons are above ground and free, but the plumule develops into a long internode under ground with scale-like leaves preceding the aerial green ones, thus agreeing to some extent with our *Podophyllum peltatum*. It is very interesting to observe the various ways in which the plumule is protected, especially when it is to hibernate in true bud form. But there does not seem to be any connection between the development of a cotyledonar tube and a naked plumule, *i. e.*, without scale-like leaves, nor between a hibernating plumule, surrounded by scale-like leaves, and free cotyledons, for in *Podophyllum peltatum* we find both; the plumule is here not only protected by the inclosing sheath of the cotyledons, but its first leaves, which are scale-like, furnish it ample protection during the winter.


FIG. 3. Young plant of *P. peltatum* in its second year; natural size.

In continuing the investigation of the seedlings of Podophyllum, we noticed the following spring that the plumule had finally developed into a few very short internodes with scale-like, membranaceous leaves (*fig. 3*, $l^1$–$l^3$), and only one green leaf *L*, with long petiole and a blade of peltate shape. The primary root still persists, and the direction of the main shoot, the only one developed so far, is vertical. In comparing the plant at this stage

with the seedling (*fig. 2*), we notice a striking resemblance to exist between the outline of the first proper leaf, *L*, and that of the united blades of the cotyledons. It seems as if the peltate form is already imitated by the cotyledons, which actually in this case represent but one leaf, when considered from a biological standpoint. This coincidence made us examine seedlings of other plants with peltate leaves, in order to ascertain whether the cotyledons of these might also imitate the shape of later developed stem leaves, but in those examined we failed to discover any that might be compared with Podophyllum. In *Menispermum Canadense*, for instance, the cotyledons are linear; in Tropaeolum the cotyledons remain under ground and inclosed by the seed-coat; *Hydrocotyle vulgaris* has small ovate cotyledons; and both Victoria and Nelumbium have their cotyledons remaining in the seed even a long time after germination has taken place.

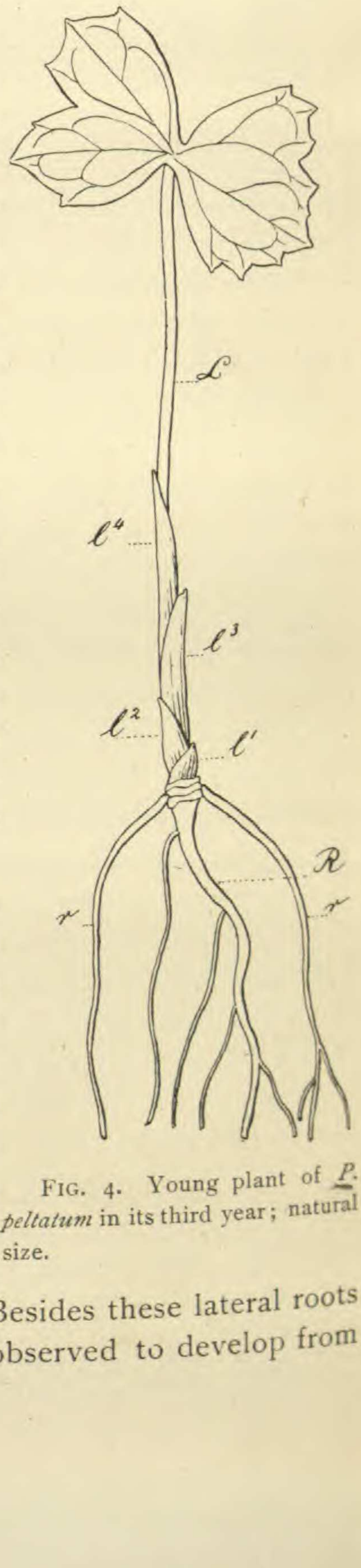



FIG. 4. Young plant of *P. peltatum* in its third year; natural size.

When the young plant of Podophyllum has passed the first two years of its existence, it sends up a long petioled leaf (*fig. 4*, *L*), with a blade that is considerably larger and more deeply lobed than the leaf shown in *fig. 3*. The development of a few scale leaves ($l^1$–$l^4$) preceding the green one is also noticed at this stage, and the primary root, *R*, still remains with an increased number of lateral roots. Besides these lateral roots the first pair of secondary roots, *r*, is observed to develop from

the rhizome, which is here represented by the short internodes of the preceding year's growth, with scars remaining of the first scale leaves, $l^1$–$l^3$, and the first aerial green one, $L$. The direction of this little rhizome is still vertical, and the arrangement of the leaves is strictly alternate, in conformity with those of the previous year.

By examining the leaf axils of these two stages (*figs. 3* and *4*), we found no buds, excepting a very minute one in the sheathing base of the aerial leaf (*fig. 5*). This bud being terminal and the only one on the rhizome continues its growth for several years, developing successively a few scale leaves and a single green aerial one at the same time. It is not until the plant has reached an age of four or five years, that a lateral bud appears in the axil of one of the scale leaves and grows out as a horizontal shoot with elongated internodes. From this period the terminal bud of the mother-shoot ceases to grow, but remains dormant, and ready to push out should the lateral shoot become injured.

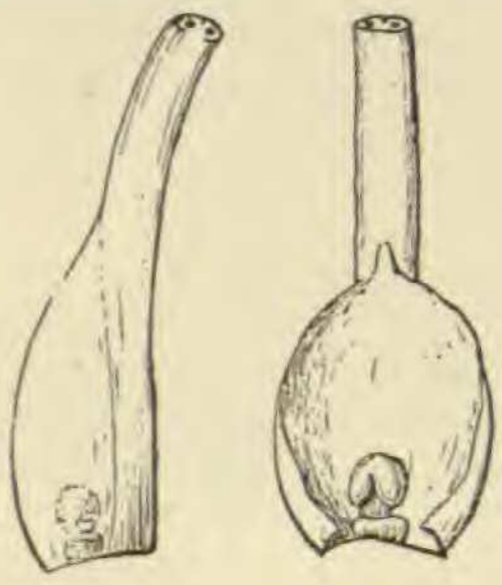


FIG. 5. Base of petiole of a leaf from a young plant; seen from the side and front; the sheath laid open to show the bud; magnified.

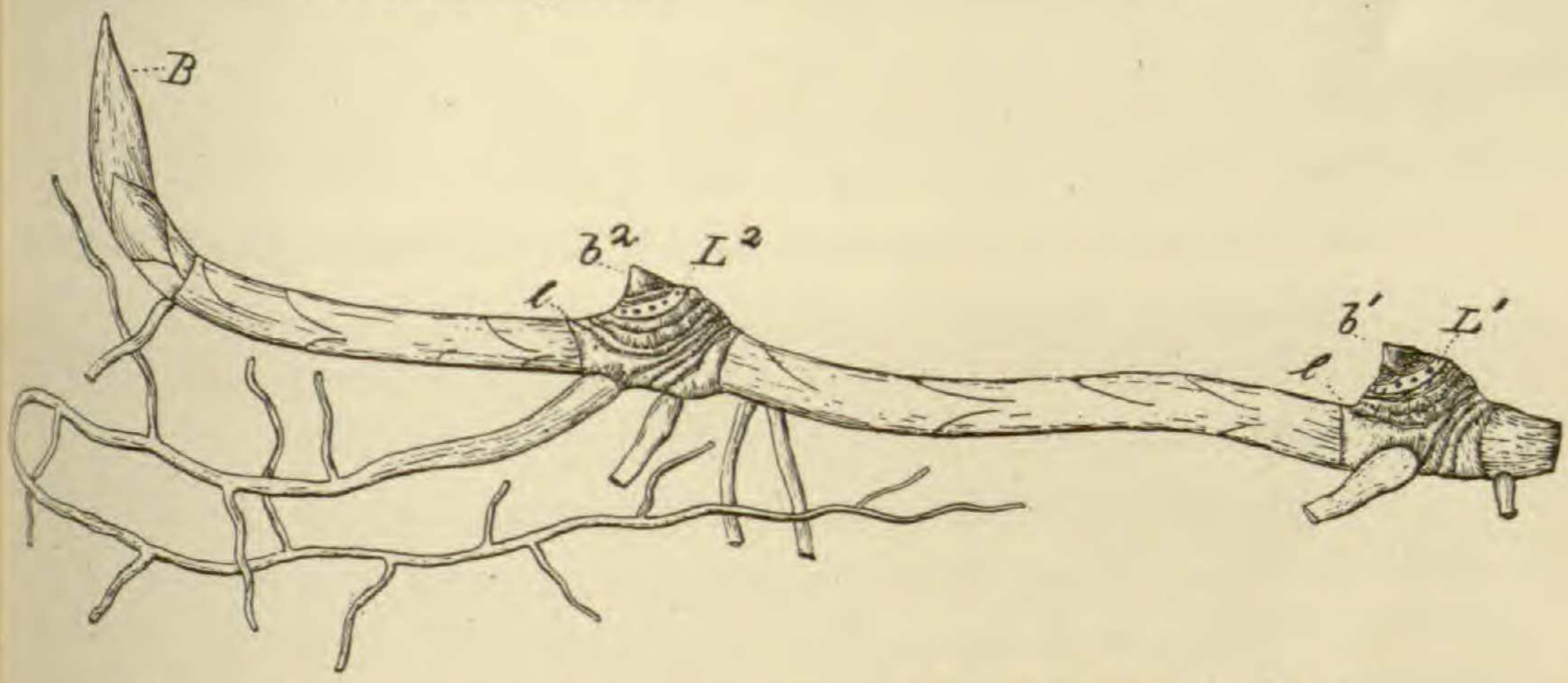



FIG. 6. Rhizome of full-grown specimen of *P. peltatum;* natural size.

When the lateral bud develops, the direction of the rhizome becomes changed from vertical to horizontal, and the original monopodium passes over into a sympodium. The accompanying figure (*fig. 6*) shows the rhizome of a mature plant,

representing three years of growth: $b^1$ being the terminal bud from 1897, $b^2$ the corresponding one from 1898, while the large bud, *B*, the terminal one of the entire rhizome, will develop in the spring of 1899. $L^1$ and $L^2$ indicate the scars of aerial leaves borne upon shoots which are terminated by dormant buds, $b^1$ and $b^2$. The scars left from the scale leaves form narrow dark lines on the rhizome, but are very distinct on the short as well as on the elongated internodes. In the accompanying drawing of a joint of a mature rhizome of Podophyllum (*fig. 7*), the dis-

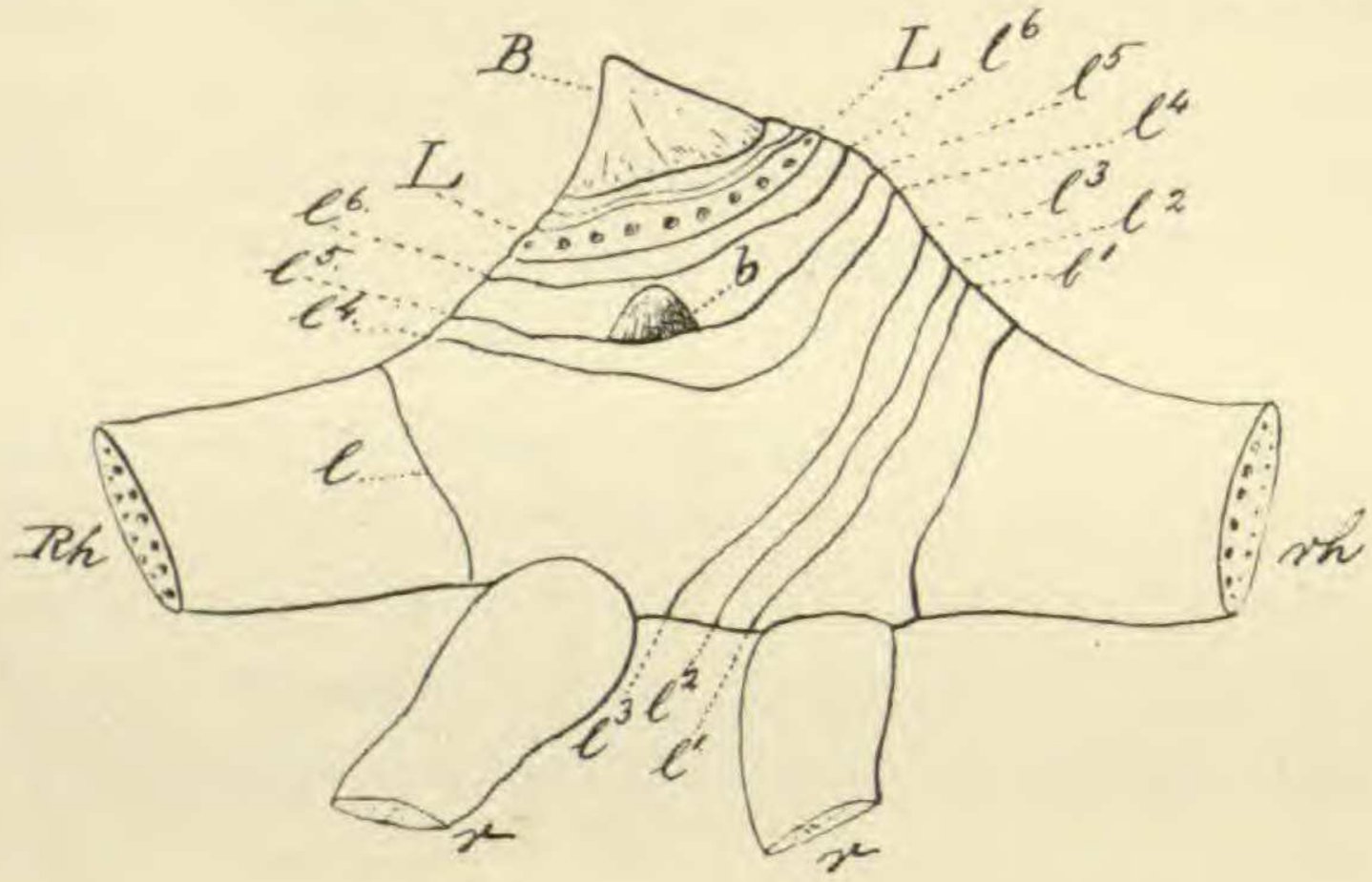



FIG. 7. Part of rhizome; magnified.

position of the leaves and buds may be seen more plainly. *Rh* and *rh* represent the anterior and the posterior parts of the rhizome; $l$–$l^6$ indicate the scars from scale leaves, while *L* shows the scar from a green leaf; *B* and *b* are buds, terminal and lateral; *r* and *r* are secondary roots.

As we have stated above, the ramification of the rhizome is sympodial, a fact that is readily observed if we examine *fig. 7*. All the scale leaves, excepting the one marked *l*, are situated upon the same axis, terminated by the larger bud, *B*, which is purely vegetative and remains dormant. The anterior part of the rhizome, *Rh*, however, which bears a scale leaf, *l*, has developed from the axil of the scale leaf, $l^3$, in the same manner as the smaller bud, *b*, in the axil of the scale leaf, $l^5$. But while the smaller bud, *b*, seldom develops any further, the branch, *Rh*, grows

out horizontally and in the same direction as the older part of the rhizome, as if it were the main axis itself. The entire rhizome thus represents a sympodium, composed of a series of shoots, each of which is terminated by a vegetative bud, *B*, and represents actually a monopodium.

In considering the arrangement of the leaves, we notice a very peculiar disposition. The diagram, *fig. 8*, is taken from a part of the rhizome corresponding to that shown in *fig. 7*, with the exception that instead of a green leaf, as at *L*, we have a flower-bearing stem with two leaves, $L^1$ and $L^2$, next to the terminal bud, *B*. All the leaves are alternate, but while the two outermost, $l^1$ and $l^2$, are situated to the right and left of the axis, the four innermost, $l^3$–$l^6$, are turned about 45° to the left of the median plane of the axis. Three buds are visible in this diagram, the terminal, *B*, and two lateral, $b^1$ and $b^2$, which are not strictly axillary, but have become pushed a little to the side, especially $b^2$.

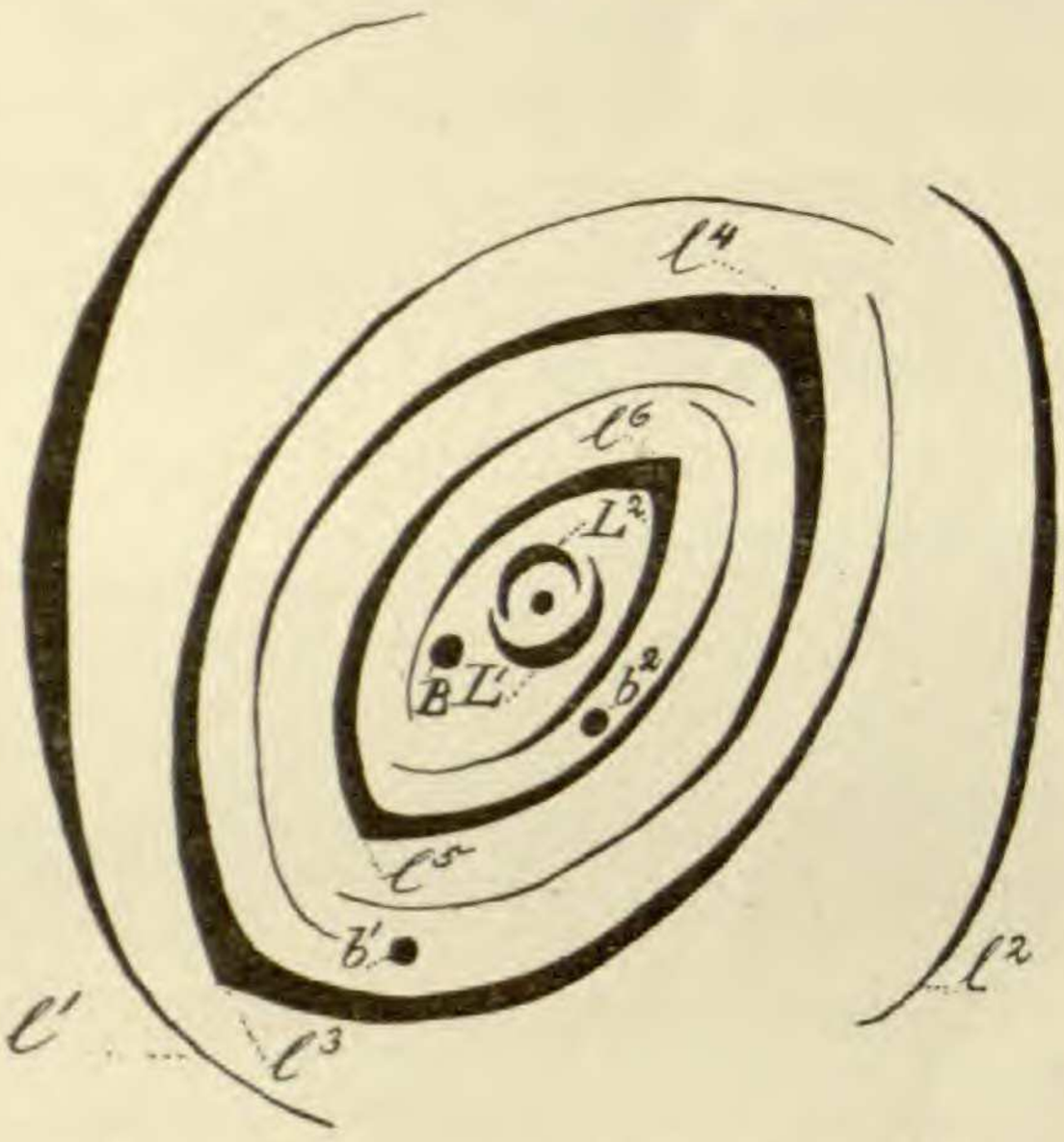



FIG. 8. Diagram of shoot of *P. peltatum*. *B*, terminal, $b^1$ and $b^2$ axillary buds; $l^1$—$l^6$, scale leaves; $L^1$ and $L^2$, the two green stem leaves.

As stated above, the terminal bud remains dormant, while the bud, $b^1$, from the scale leaf $l^3$, grows out as a long, horizontal shoot, continuing the direction of the rhizome. The bud, $b^2$, which is developed in the axil of leaf $l^5$, also remains frequently dormant. While this structure, as shown in the diagram, *fig. 8*, appears to be the most common in our plant,[3] we have noticed, that some variations exist, *e. g.*,

[3] By comparing Professor Schumann's observations with ours on the rhizome of *Podophyllum peltatum*, we have noticed several important discordances. Our very considerable and fresh material from the vicinity of Washington, D. C., showed, however, the structure as described above, and it may be that Professor Schumann's material, cultivated at Berlin, did not represent as typical development of buds and leaves as our specimens, grown wild in the native country of this plant.

an axillary bud may be developed from leaf $l^4$, instead of from leaf $l^5$. Also, a bifurcation is not uncommon, and this depends upon the non-development of the large bud, $b^1$, which is then replaced by two other buds in the axils of leaves $l^4$ and $l^5$, both of which are then situated to the right and left of the axis. These two buds develop simultaneously into two horizontal branches, with elongated internodes. Furthermore a bud may be developed in the axil of the leaf $l^1$, but remain dormant. When the large bud, $b^1$, beccmes injured, two different cases were observed in which the rhizome nevertheless became able to continue its growth. Either a bud developed from leaf $l^4$, to grow out and replace the normal continuation of the rhizome, or the terminal bud, *B*, ceased to be dormant, developing into a horizontal branch. This last case is figured in the accompanying drawing (*fig. 9*). There are three relatively short internodes with scale leaves, terminated by a large bud, which contains a floral axis and some vegetative buds. The age of this branch is three years. The first internodes show a tendency to become stretched like those of the sympodial shoot when it develops. That the terminal bud became developed in this case was merely due to the injury of the shoot $b^1$, as is to be seen in *fig. 9*. A still more peculiar case may occur when the bud, $b^1$, does not grow out as a long branch, but as a few very short internodes, simulating the one described above.

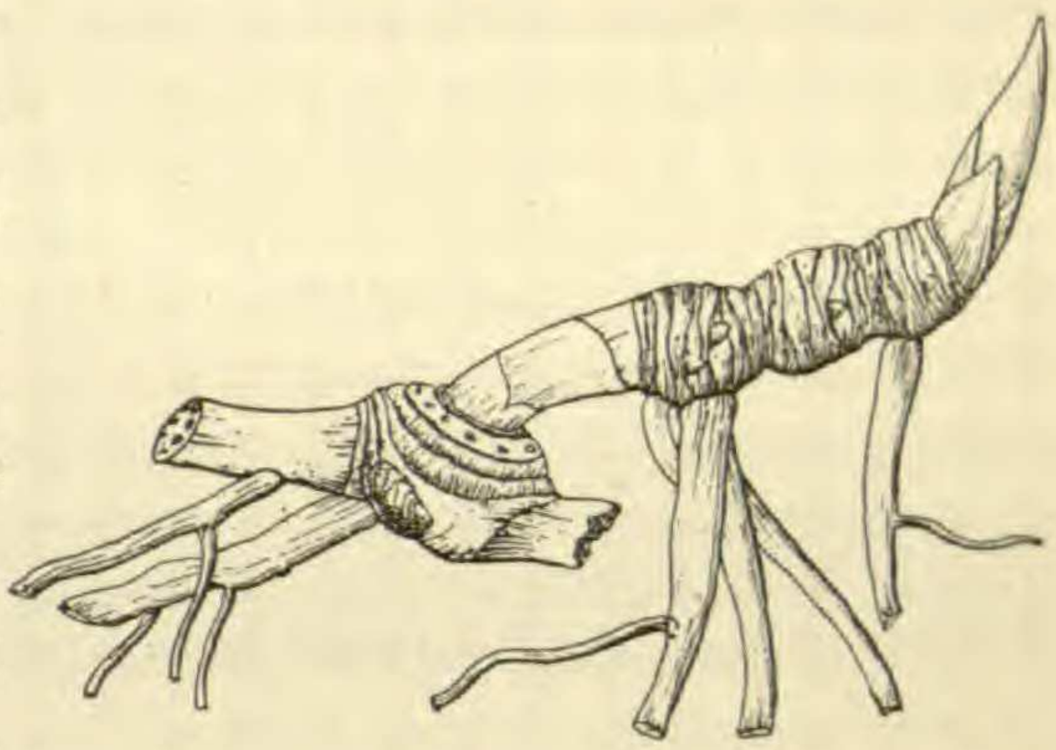


FIG. 9. Rhizome of *P. peltatum;* the terminal bud has grown out into a horizontal branch; natural size.

The development of these buds is, therefore, not restricted to any of the scale-like leaves, excepting the leaf, $l^2$; neither is their position constant, although the majority of cases examined show that a frontal position is the most common and naturally the most advantageous to the plant.

It now remains to mention the position of the floral axis.

The flower-bearing stem of *Podophyllum peltatum* develops exclusively from one of the short internodes of the rhizome, and is axillary, never terminal. It invariably develops, so far as noticed, from the axil of the leaf, $l^6$, while the terminal bud remains dormant at the base of its frontal part. By the continued growth of the flower-bearing stem, the terminal bud fuses with this and becomes almost imbedded in its basal portion. The two stem leaves, $L^1$ and $L^2$, are situated to the right and left of the flower, occupying a position that corresponds very well to that of two prophylla, as these occur in the dicotyledons, an explanation that has been proposed by Eichler (*l. c.*).

Concerning the structure of a floral bud, it is interesting to notice that sometimes one of the scale leaves may have a small peltate blade developed, as shown in *fig.* 10, *a*. The scale leaves are somewhat fleshy and surround the very minute flowering stem. Of its two leaves, the one is developed earlier than the other. The base of the petiole of this leaf is dilated into a pair of broad wing-like stipules, *St*, which overlap each other and enclose a very small green leaf and a flower bud (*fig.* 10, *b*); thus the two green leaves of Podophyllum did not develop at the same time, as it might seem, when we examine the plant during its flowering period with the leaves apparently opposite.

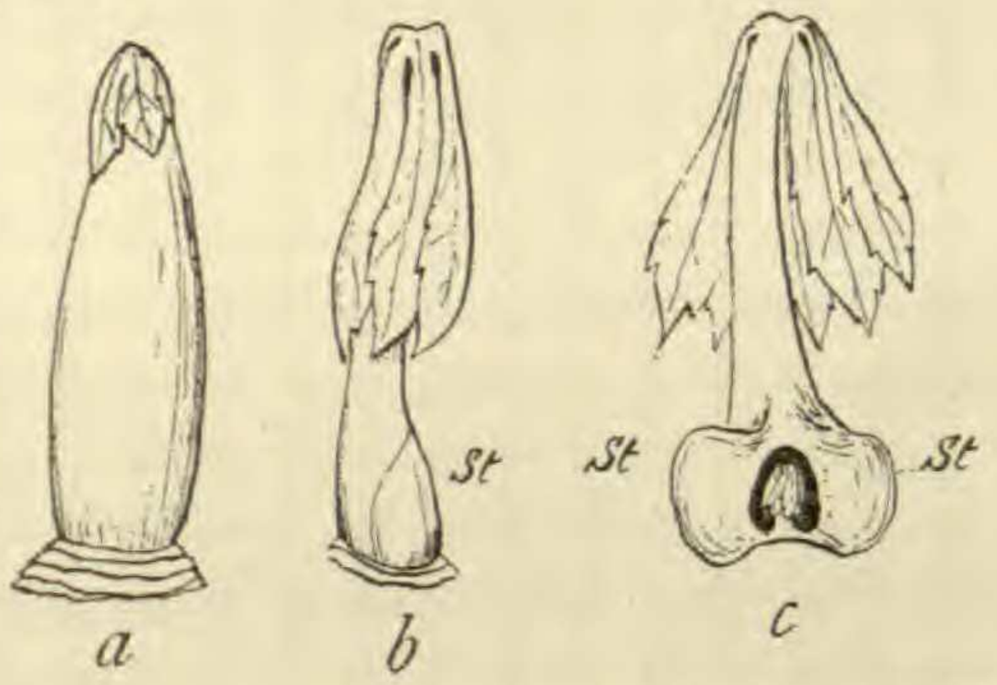



FIG. 10. *a*, scale leaf with small peltate blade; *b*, first stem-leaf enclosing the second one in its basal sheath; *c*, same, the sheath laid open to show the enclosed leaf and flower-bud; magnified.

The roots are very strong and somewhat thickened. They develop exclusively from the short internodes of the rhizome, close to the lower surface, from which they proceed horizontally close to the surface of the soil.

The anatomy of *Podophyllum peltatum* in some respects resembles that of the monocotyledons more than it does that of the dicotyledons. De Bary has, therefore, classified Podophyllum

among anomalous dicotyledons, in which the mestome bundles of the aerial stem are not arranged in concentric bands. It is strange to notice that Podophyllum has this feature in common with Diphylleia, Leontice, and various species of Papaver, Thalictrum, and Actæa.

A transverse section of the stem above ground shows a thin walled epidermis and a cortical parenchyma that passes over into the large pith, both of which consist of thin walled cells of nearly the same size. The mestome bundles form three irregular bands, the two inner ones being located in the pith, and represent various stages of development. Very characteristic is the structure of the leptome, in which we notice no other elements than sieve tubes and their companion cells, while cribral parenchyma is totally absent. In this respect Podophyllum agrees with the monocotyledons and the Ranunculaceæ only among the dicotyledonous orders. The hadrome consists of a number of vessels arranged very close to each other, and a well developed cambium is noticeable between this part of the mestome bundle and the leptome. Stereome forms closed rings around the mestome bundles; it is especially thick walled on the leptome side.

By comparing the structure of the stem above ground with that of the rhizome, the following divergences were observed: The mestome bundles form only a band, and that an almost regular concentric one, with only a few small bundles lying outside in the cortex. The vessels are very thick walled. While the cortex and the pith show approximately the same development as in the aerial stem, the outer layers of the cortical parenchyma show a very pronounced thickening of the cell walls, like those of collenchyma. Sheaths of thin walled stereome surround the mestome bundles without forming connecting layers between them.

The structure of the petioles of the stem leaves shows a very irregular distribution of the mestome bundles. There is here, as in the aerial stem, an almost regular peripheral band, located in the cortex; but inside this, in the pith, the mestome bundles are

scattered very irregularly. The cylindrical petiole of a young leaf, developed from the rhizome, has only four peripheral mestome bundles in the cortex, and one in the center of the pith. Corresponding with the stem above ground, the mestome bundles of the petioles are supported by sheaths of quite thick walled stereome, especially on the leptome side.

Characteristic of the root is the strong thickening of the outer walls of the epidermis, even in roots of very young specimens. The cortex is solid, with no lacunae, and the innermost layer is differentiated into a thin walled endodermis. Five groups of vessels alternate with a corresponding number of leptome groups, bordering on the pericambium, and the innermost part of the central cylinder is occupied by a thin walled conjunctive tissue.

In considering these anatomical peculiarities, especially the structure and arrangement of the mestome bundles, it cannot be denied that Podophyllum possesses a very anomalous internal structure. The morphological characteristics which have been discussed above, the manner of germinating, and the peculiar ramification observable in the rhizome are seldom met with in dicotyledonous orders; and the creeping rhizome with its monopodial shoots reminds us very much more of the monocotyledons.

Hence, when the "mesophytes," to which our plant is said to belong, have been characterized as possessing "no very pronounced or interesting features in anatomical or morphological respects," the statement does not seem applicable to *Podophyllum peltatum*. Neither does it hold true if we examine the other herbs that constitute the vegetation in the deciduous forests of North America. Many of the herbaceous species which are generally associated with Podophyllum show morphological peculiarities that are very conspicuous and characteristic. It would, indeed, be difficult to point out a vegetation in this country that contains a larger number of herbs with as varied and interesting morphological structure as our forest plants, lately classified simply as "mesophytes." *Podophyllum peltatum* prefers the wooded belts in this country, and its nearest associates,

those that occupy the same kind of soil and grow in company with it, are, strange to say, just the genera that were once considered as representing a little natural group of plants: Diphylleia, Jeffersonia, Caulophyllum, Actæa, and Cimicifuga. These strikingly resemble one another in habit; moreover, they possess a number of biological peculiarities that might even lead to a more correct understanding of their true relationship than such small and insignificant floral characters as are used for the establishment of "orders." By taking the habit into consideration, we may sometimes reach a simple but much more natural idea of the plant and its nearest allies.

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